Title: Seed production, infestation and viability in *Acacia tortilis* (synonym: *Vachellia tortilis*) and *Acacia robusta* (synonym: *Vachellia robusta*) across the Serengeti rainfall gradient.

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Abstract

Tree recruitment in savannas proceeds in multiple stages characterized by successive filters occurring at the seed and seedling stages. The "demographic bottleneck" hypothesis suggests that such filters ultimately restrict tree density and prevent trees from dominating grasses in savannas, but many of the demographic transitions underlying this assumption have not been quantified. We investigated how short- (1-2 years) and long-term (40+ years) rainfall patterns influenced seed production, infestation and viability for two dominant species, *Acacia robusta* and *Acacia tortilis* across the Serengeti ecosystem mean annual precipitation (MAP) gradient over a two-year period. We found that neither production, nor infestation, nor viability were influenced by rainfall. Pod production differed between species and increased with tree height in *A. robusta*. Mean infestation proportion in 2013 was higher (mean ± SE; 0.28 ± 0.08) in *A. tortilis* than in *A. robusta* (0.11 ± 0.05) but the trend reversed in 2014, when *A. tortilis* (0.33 ± 0.10) had lower infestation than *A. robusta* (0.61 ± 0.09). Under laboratory conditions, *A. tortilis* and *A. robusta* seeds had maximum germination (=viability) proportions of 70 and 20%, respectively. Mean seed viability was more than five-fold higher (0.46 ± 0.19) in *A. tortilis* than in *A. robusta* (0.08 ± 0.10). Our study has produced important estimates for seed stage demographic dynamics that can be used for modelling tree dynamics in Serengeti system, and savannas in general.

Key words: Savanna, East Africa, seed demography, tree recruitment, bruchid beetles

Introduction

Tree recruitment, the process by which a seed develops into a reproductive mature tree, proceeds in a series of distinct stages such as seed production, seed dispersal, seed germination to seedling establishment and growth (Harcombe 1987; Midgley and Bond 2001). Each of these stages is shaped by various sources of mortality. These mortality filters include limited seed production (Ashman et al. 2004; Knight et al. 2005); dispersal limitation (Nathan and Muller-Landau 2000; Salazar et al. 2011); seed predation (Barnes 2001; Goheen et al. 2004) and/or seed infestation by pests (Lamprey et al. 1974; Miller 1996). The prevalence and intensity of these mortality drivers vary spatially and temporally, with heterogeneity in canopy structure and site conditions being among important sources of variation in survival for a developing individual, especially in forest ecosystems (LePage et al. 2000; Wyatt and Silman 2004).

Although seed limitation has received significant attention in forest ecosystems around the globe (Svenning and Wright 2005; Clark et al. 2013; Luo et al. 2013), there have been few comprehensive studies that can assess how seed availability and mortality at various stages affect recruitment in savanna ecosystems, especially in conjunction with variation in rainfall. Most empirical studies examining the drivers of savanna vegetation structure tend to focus almost exclusively on recruitment and survival processes at the post-germination stages (Goheen et al. 2004; Sankaran et al. 2004; February et al. 2013). Consequently, the "demographic bottleneck" hypothesis, which posits that early savanna tree stages experience high rates of mortality and therefore tree recruitment is rare and episodic (Sankaran et al. 2004; Sankaran et al. 2005; Bond 2008), is often informed by what happens at the seedling rather than the seed stage (Midgley and Bond 2001). The

demographic transitions that occur at the seed stage, however, potentially comprise an important component of the demographic bottleneck hypothesis but have not been quantified to the same extent as transitions at the seedling stage. Some potential factors (or filters) that contribute to the occurrence of a demographic bottleneck in savannas include: 1) limited seed production and pre-dispersal predation (Greene and Johnson 1994; Ashman et al. 2004); 2) infestation by beetle larvae or other parasites (Lamprey et al. 1974; Miller 1996; Rodríguez-Pérez et al. 2011), leading to reduced seed viability; 3) dispersal limitation (Nathan and Muller-Landau 2000; Salazar et al. 2011) and 4) post-dispersal predation by baboons and monkeys (Barnes 2001), rodents (Goheen et al. 2004), birds (Linzey and Washok 2000) and invertebrates (Hulme 1998; Shaw et al. 2002). As seeds are subjected to the above-mentioned filters in sequence, their effects can accumulate, potentially limiting the supply of individuals to later demographic stages, and ultimately affecting tree abundance at local and regional scales (Münzbergová and Herben 2005).

While past studies have shown that spatial and temporal variation in seed bank size in savanna trees has potential importance for understanding woody plant dynamics and the spread of tree encroachment (Witkowski and Garner 2000; Walters and Milton 2003), the overall effect of rainfall on the various filters identified above (e.g. seed infestation, seed production and viability) remains poorly understood. This is an important gap, given that mean annual precipitation is the only consistent environmental correlate of tree cover across the savanna biome (Sankaran et al. 2005; Bucini and Hanan 2007).

This study had two primary objectives: 1) to quantify three key processes (seed production, infestation, and viability) that drive demographic rates at the seed stage of

tree recruitment in two savanna tree species, and 2) to investigate how these processes vary with short term (1-2 years) and long term (40+ years) variation in rainfall in the Serengeti ecosystem of East Africa. Our first objective forms part of a broader effort by our research team to develop estimators for key demographic processes describing tree demography in Serengeti. Ultimately, these estimators will allow us to model the dynamics of the system. To accomplish our objectives, we quantified seed pod production, infestation and viability for two dominant savanna species – *Acacia robusta* and *Acacia tortilis* – at 10 sites spanning the Serengeti's mean annual precipitation (*MAP*) gradient. These two species belong to the genus *Acacia*, recently re-typified as *Vachelia* (Kyalangalilwa et al. 2013). However, the name *Acacia* is used here to maintain consistency with past work from our group and others (Moore et al. 2011; Thiele et al. 2011; Miller et al. 2014).

A previous study in this ecosystem (Rugemalila et al. 2016) showed that MAP plays a major role in determining tree species compositional change: communities transition from being dominated by *A. tortilis* to *A. robusta* from the dry to the mesic end of the precipitation gradient. Our main interest in the present study is to examine whether rainfall influences demographic processes at the seed stage. We addressed whether the replacement of *A. tortilis* by *A. robusta* with increasing precipitation relates to pre-germination constraints such as seed production, infestation and/or viability. We hypothesized that *A. tortilis* would have high infestation at high rainfall sites and that *A. robusta* seed production, germination and viability would be limited by water at the dry end of the gradient. As seed mass and tree height in woodland communities are among the factors that reflect adaptation to local environments and competition capabilities

(Thomson et al. 2010; Thomson et al. 2011), we investigated the association between demographic processes and seed mass and how the latter vary between species and across the MAP gradient.

Methods

Study system and species

The study was conducted in the Serengeti National Park (Serengeti - hereafter) in northern Tanzania – East Africa (Fig. 1). Serengeti has a total area of ~14,760 km^2 and is part of a larger ~30,000 km^2 ecosystem that extends to southwestern parts of Kenya's Maasai Mara. Serengeti lies between 1–2° S, 34–26° E and is buffered by protected areas and game reserves. Elevation ranges from ~920 m to ~1,850 m and MAP ranges between ≥500 mm. yr^{-1} in the SE to ~1100 mm. yr^{-1} in the NW near Lake Victoria. Rainfall is seasonal, with a wet period normally from November to June and a dry period from July to October (Sinclair et al. 2000). Woody vegetation in Serengeti is dominated by *A. robusta* and *A. tortilis,* followed in relative abundance by *Acacia drepanolobium (*synonym: *Vachellia drepanolobium), Acacia senegal (*synonym: *Senegalia senegal), Commiphora trothae* and *Balanites aegyptica* (Anderson et al. 2015). Detailed description of Serengeti vegetation, soils and rainfall characteristics can be found elsewhere (Dempewolf et al. 2007; Holdo et al. 2009; Anderson et al. 2015). Our study focused on the two most abundant overstorey tree species: *A. tortilis* and *A. robusta* (Anderson et al. 2015). The former, also known as the "umbrella acacia", is a medium to large-sized tree producing pods that are variable in size and are indehiscent (pods do not open to expose their seeds while on the tree). In East Africa, *A. tortilis* seed production peaks between October and December (Loth et al. 2005). This species has a broad

geographic range, being widespread throughout Africa and the Middle East and locally abundant in Serengeti. *Acacia robusta* is a single-stemmed, fairly high-branching tree that produces dark brown pods that are dehiscent (pods open and disperse seeds while on the tree (Gordon-Gray 1965)), and may remain on the tree for long periods. These two species were originally targeted because of their large spatial extent and relative dominance across most of Serengeti and because of their differing population trends, with *A. tortilis* declining, and *A. robusta* increasing in abundance across the ecosystem's MAP gradient (Anderson et al. 2015; Rugemalila et al. 2016).

Seed pod production

We measured tree productivity using a network of permanent vegetation plots established in 2009 (Holdo et al. 2014). There are 10 sites (variable *SITE*), each with four 20 × 50 m plots (variable *PLOT*), except for the Ngorongoro Conservation Authority [NCA] site, which has two plots, resulting in a total of 38 plots distributed across the Serengeti landscape (Fig. 1). The sites were representative of the major *Acacia*-dominated habitats of Serengeti. Our study utilized the 19 plots (2 plots in each of nine sites and one NCA plot) that were protected from fire. Each plot was visited at least once a month between January 2013 and July 2014 to collect data and track phenology (flowering and pod production) in trees. In Serengeti, tree reproductive phenology is spatially patchy and not all trees produce pods every season (Lamprey et al. 1974; Mduma et al. 2007). Therefore, on each visit, we scored each individual tree > 2 m in height for presence or absence of seeded pods to obtain the proportion of reproducing trees. Tree surveys at each plot were conducted annually to obtain height (variable *HEIGHT*), recorded using a Nikon Forestry PRO Laser Hypsometer and basal diameter (variable *BASAL*) for each tree, measured

with Haglöf Mantax calipers (Forestry Suppliers, Inc., Jackson, MS). Tree survey data were collected in 2013.

Seed infestation

To investigate seed infestation and viability across rainfall gradient, we identified sets of five randomly-chosen mature trees per species per site (*i.e.* 10 trees per site - if both species present, otherwise 5 trees) for seed collection during two separate periods between January 2013 and August 2014. We tagged and mapped selected trees with racetrack aluminum tags (Forestry Supplier Inc. USA) and GPS respectively. We collected pods by shaking and/or knocking branch tips with a light-weight PVC pipe to allow pods to fall onto a tarpaulin placed on the ground, under tree canopy. We transported pods to the Serengeti Wildlife Research Center and sun-dried them for 3-5 days before manual seed removal. After sun-drying and cleaning for debris and litter, we sorted subsets of seeds to obtain the proportion of infested seeds per tree (variable *INFESTATION*). Seeds were classified as infested when entry/exit holes made by bruchid beetles were clearly visible on their seed coat (Loth et al. 2005; De Menezes et al. 2010). We stored sorted seeds at room temperature for 2 to 4 weeks and then checked them again for new infestations not detected during the first sorting event.

Seed viability

Here, we define viability as a potential of seeds to germinate under ideal conditions. We investigated the relationship between seed viability *(*variable *VIABILITY),* *INFESTATION*, *MAP* and mean current precipitation (*MCP* – defined as the mean annual rainfall during the study period) by conducting laboratory germination trials under

158 uniform conditions at the Serengeti Wildlife Research Center in central Serengeti. For
159 each species, infested and non-infested seeds were planted separately into germination
160 trays (28 cell - 6 cm deep tray) containing soil collected inside the park. To improve soil
161 porosity, we added sand in a well-mixed 2:1 soil-sand ratio, homogenized by hand and
162 sieved. During the homogenization and sieving process, we took care to ensure that the
163 soil was free from debris and other seeds. In each germination tray cell, we planted one
164 seed and covered it with soil at a depth of about one seed length and watered daily. The
165 amount of water used was just enough to keep the soil moist but not waterlogged. For
166 each species, we randomly selected 100 infested and non-infested seeds from each site
167 (fewer if sample sizes were insufficient). The total number of seeds and their distribution
168 by species, infestation status and the totals are summarized in Table 1. We scarified all
169 non-infested seeds to expose the seed mesocarp and hence enhance water permeability,
170 either by nicking the seed-coat with a razor blade or gently scratching using sand paper
171 (the method depended on the efficiency to the user). It should be noted that germination
172 rates following scarification capture germination potential, not necessarily germination
173 under field conditions, which are known to be low (Danthu et al. 1992; Mucunguzi and
174 Oryem-Origa 1996; Danthu et al. 2003). We did not scarify infested seeds as the bruchid
175 exit holes allow water uptake by the seed (Lamprey et al. 1974). We inspected the
176 germination trays every day for evidence of seed germination for 35 days following the
177 initial planting. The seed was considered viable after it produced cotyledons above the
178 soil surface.

179 **Rainfall**

We investigated the role of recent rainfall amounts (as opposed to long-term trends) with rainfall data collected in years 2013 and 2014 from our network of digital weather stations installed across the Serengeti rainfall gradient, associated with each of the 10 study sites. Rainfall was quantified hourly at each weather station with an ECRN-100 0.2 mm resolution tipping spoon rain gauge (Decagon Devices, Pullman WA). To capture moisture influence on seed variables, we averaged monthly cumulative rainfall values (*MCP*), beginning six months prior to the start of seed collection for each collection season. For long term rainfall data, we used a GIS layer containing interpolated rain gauge data for Serengeti for the period of 1960 – 2006 (Anderson et al. 2015). We extracted *MAP* values for every individual tree and plot location using ArcMap 10.2.2 (ESRI 2013).

Data analysis

We used a model selection approach (Burnham and Anderson 2002) to identify important explanatory covariates for most of our analyses, using AIC to compare the fits of alternative candidate models. In several cases, we included year of collection (variable *YEAR*) as a covariate. Normally this variable would be treated as a random effect, but here we treated it as a fixed effect because we were interested in detecting differences between years and any year by environment interaction. To quantify the relationship between precipitation and seed pod production, we first computed site-level proportions of pod production for *A. robusta* and *A. tortilis* and plotted production proportion as a function of both *MAP* and *MCP*. A visual inspection of the phenology data suggested no clear relationship between pod production and either *MAP* or *MCP* for either species

(Fig. 2). As a result, we did not use moisture variables in the model selection approach. Instead, we focused on characterizing the relationship between pod production and tree size, given that one of our long-term research goals is to develop suitable estimators for all demographic processes in the Serengeti tree life cycle, and that seed production is likely to be strongly determined by tree size. We developed a set of five candidate models containing combinations of tree height (*HEIGHT*), basal area (*BASAL*) and species (*SPECIES*) as fixed effects, with *SITE* and *PLOT* as a random effect with a binomial error distribution. We fit our candidate models with the *glmer* function in the *lme4* package in R. Our initial results indicated that an interaction between *SPECIES* and *HEIGHT* (Table 2) explained the variation in pod production; therefore, we performed a separate linear regression for pod production as a function of tree height for each species.

For the infestation analysis, we initially treated individual trees as units of observation and fit our models with *glmer*, assuming a binomial error and treating *SITE* as a random effect. The models were highly overdispersed, however, so we instead calculated logit-transformed (Baum 2008; Warton and Hui 2011) infestation proportions for further analysis. To explore the effects of *MAP*, *MCP*, *SPECIES* and *YEAR* of collection on infestation proportions, we developed eight candidate models combining main effects and interaction effects of interest (Table 3). To assess whether infestation proportions were associated with *MCP*, we developed two additional sets of six candidate models each (Table 3), applying *MCP* on infestation data corresponding with year of seed collection, as above. We compared model fits with the *lme* function in the *nlme* package in R (Pinheiro et al. 2011) using *SITE* as a random effect.

For the viability analysis, we used the cumulative number of germinated (N_c) and ungerminated ($N_{initial}$ - N_c) seeds at the end of the 35-day trial period as the response variable in a logistic regression. We first produced plots of daily cumulative proportion of seeds germinated over time, which suggested non-saturation in three of the year curves from 2013 for *A. tortilis* (*i.e.*, germination had not ceased entirely in those cases). To test whether non-saturation might affect our conclusions, we produced a second dataset using the asymptote of a Michaelis-Menten function (Michaelis and Menten 1913; Johnson and Goody 2011) fitted in R using the *nls* function (R Development Core Team 2011) as the estimated maximum germination proportion. We back-transformed this proportion into the asymptotic cumulative number of germinated seeds (N_{asym}), to be used with ($N_{initial}$ – N_{asym}) as the binomial response variables in a second logistic regression. We compared the fits of alternative candidate models in four separate analyses using *glmer* with a binomial error distribution. The candidate models included main effects of *MAP*, *SPECIES* and/or *INFESTATION*, plus other targeted interaction effects (Table 4). To better understand the mechanistic basis of any variation in germination potential *(VIABILITY)*, we first computed the mean seed mass between species for infested and non-infested seeds. We then assessed the relationship between seed mass and rainfall by testing for the effects of *MAP*, (plus *MCP*), *YEAR* and *SPECIES* on seed mass using candidate models (Appendix 2) fitted with linear mixed-effects models implemented with *lme*.

Results

Over the two-year period of study, we collected data from 258 individual trees of the two-focal species for the pod production study (Appendix 1). There was no relationship

247 between the proportion of pod producing trees and either *MAP* or *MCP* for either species
248 (Fig. 2). Models containing species and height effects provided the best fit for predicting
249 proportion of pod producing trees. The species effect alone did not improve model fit
250 over an intercept model, but the addition of tree height (a positive effect) improved fit
251 over the species-only model (Table 2). The *SPECIES* × *HEIGHT* interaction suggested
252 that pod production increased with tree height in *A. robusta* but not in *A. tortilis* (Table
253 2).

254 The proportion of seeds infested with bruchid beetles differed between tree species
255 within years, with *A. tortilis* seeds showing higher infestation than *A. robusta* in 2013, but
256 the pattern was reversed in 2014 (Fig 3). The mean infestation proportion in 2013 for *A.*
257 *tortilis* was more than twice as high (mean ± SE: 0.28 ± 0.08, n = 30) as that of *A.*
258 *robusta* (0.11 ± 0.05; n =40). The mean infestation rate in 2014 was lower in *A. tortilis*
259 (0.33 ± 0.10; n = 21) than in *A. robusta* (0.61 ± 0.09, n = 31). While mean infestation
260 proportion in *A. robusta* increased almost six fold from (0.11 ± 0.05) in 2013 to (0.61 ±
261 0.09) in 2014, there was no significant change between 2013-2014 for *A. tortilis*. Model
262 selection results from the first set of models assessing the effect of *MAP*, *SPECIES*,
263 *YEAR* and their interaction on infestation suggested that only the interaction between
264 *SPECIES* and *YEAR* explained differences in infestation among sites (Table 3). This
265 suggests that seed infestation among tree species is not consistent, but varies over time. In
266 a separate analysis, to tease apart the short- *vs* long-term rainfall effects on infestation for
267 each year, we developed two sets of additional models. The results suggested that *MCP*
268 did not improve model fit either alone or in combination with any other covariates. In

both years, the best-fitting model contained a species-effect only, with no effect of rainfall (*MAP* nor *MCP;* Table 3).

Non-infested seeds for both species showed higher viability than infested seeds, though some infested seeds were nonetheless viable (*i.e*., germination rates were nonzero). Non-infested *A. tortilis* seeds had germination proportion of about 70% while *A. robusta* seldom exceeded 20%, suggesting that, *A. tortilis* has a higher germination potential than *A. robusta* (Fig. 3). Overall, for both years, average seed viability was more than five-fold higher in *A. tortilis* (0.46 ± 0.19) than in *A. robusta* (0.08 ± 0.10). The models containing either *YEAR* or the interaction between *SPECIES* and *INFESTATION* status predicted seed viability. To investigate the importance of each variable in the absence of the other, we subset our data by *YEAR* and then by *INFESTATION* status. After analyzing each year separately, model selection results suggested that *SPECIES* and *INFESTATION* status explained differences in viability among sites for both years (Table 4). The model with species effect only, did not improve fit compared to an intercept-only model, suggesting that variation in viability is independent of species type. Further analysis using *MCP* with non-infested seeds showed that variation in viability depended on species, suggesting that site rainfall history does not influence seed viability.

In the analysis of seed mass, *A. robusta* seeds were consistently heavier than *A. tortilis* regardless of infestation status (Appendix 3). However, model selection suggested that seed mass depended on the interaction between *SPECIES, INFESTATION* and *YEAR.* To tease apart this three-way interaction, we subset the data first by species and fit a single model in each case, with main effects for *MAP* and infestation (plus their

292 interaction) and a main effect for year of collection. For both species, likelihood ratio test
293 results showed negative effects of infestation on seed mass ($P<0.0001$), and a negative
294 effect of *MAP* on seed mass in *A. tortilis* ($P<0.02$), but not *A. robusta* ($P=0.4$) (Fig 5). We
295 then subset data by *YEAR* and developed models with first the main effect of *SPECIES*,
296 *INFESTATION* and *MCP*, and then with main effects of *SPECIES* and *MCP* on non-
297 infested seed mass. Our results suggested that in the presence of infested seeds, seed mass
298 depended on the interaction between species and infestation status. In the absence of
299 infested seeds, seed mass depended on species. In all cases, rainfall variables did not
300 improve models fits (Appendix 2)

301 **Discussion**

302 Our results suggest that tree pod production, seed infestation and seed viability, which are
303 part of the early stages of tree recruitment, differ between *Acacia* species and that they
304 are not influenced by variation in rainfall across the Serengeti. For pod production, we
305 expected that the proportion of reproducing trees would increase with *MAP* or *MCP*, but
306 our results did not support this prediction. Previous studies from other tree communities
307 provide mixed evidence for the role of rainfall on tree seed production. For example, a
308 study by Seghieri et al. (1995) in northern Cameroon and another by Williams et al.
309 (1999) in Australian savannas reported that, rainfall was an important limiting resource
310 for fruit phenology in woody plants but did not create an exclusive trigger for fruiting
311 timing. Given that plant growth is water limited in savannas (Greene and Johnson 1994;
312 Salazar et al. 2011), we expected mesic sites to have greater proportions of reproducing
313 trees than dry sites. We theorize that either tree reproduction is related to plant
314 physiological adaptation and trade-offs between seed viability and water use regardless of

315 the rainfall quantity, or that the rainfall gradient in Serengeti is too wet to show the effect
316 of rainfall on seed production observed in drier systems (cf. Andersen et al. (2016)).
317 *Acacia* species are known for their adaptation to seasonal rains and tolerance to long dry
318 periods (Kebbas et al. 2015) and other savanna trees tend to avoid seasonal water
319 dependence by either avoiding water loss through scleromorphic features or the use of
320 water stored in the deep soil profile (De Bie et al. 1998).

321 While our results suggested no relationship between the proportion of podded trees
322 and either precipitation variable (*MAP* and *MCP*), pod production variation was
323 explained by the interaction between species and tree height (Table 2). A separate
324 analysis for each species suggested that the proportion of reproducing trees increases with
325 tree height in *A. robusta* but not in *A. tortilis*. We hypothesize that tree reproduction in
326 the Serengeti is determined by species functional and physiological traits rather than
327 environmental variables. These traits could be important for trade-offs associated with
328 seed dispersal strategies. For example, as previously defined (*see* methods), *A. robusta*
329 and *A. tortilis* species are dehiscent and indehiscent, respectively. As dispersal in *A.*
330 *robusta* relies mostly on wind or self-release by gravity, it is likely beneficial for trees to
331 invest in stem height to maximize seed dispersal distance. In contrary, *A. tortilis* seeds are
332 adapted for dispersal by vertebrates due to the high nutrient content and strong scent of
333 seeds (Miller and Coe 1993); thus, low heights may be advantageous for enabling
334 consumption and dispersal by vertebrates (Or and Ward 2003). Another potential effect
335 of tree height is through infestation vulnerability by bruchid beetles, where *A. tortilis*
336 canopy seeds have been reported in the dry eastern Sahara to be less infested compared to
337 those on the ground (Andersen et al. 2016).

Our results also suggest that bruchid beetle infestation varies considerably by species and year (Fig. 3). Seed infestation has been reported to affect seed germination (Mucunguzi 1995; Miller 1996; Ahmed 2008) and tree recruitment (Rohner and Ward 1999) in other ecosystems. In this study, we predicted higher infestation in mesic sites than in dry sites because in tropical ecosystems, studies show that mesic sites which are mostly characterized by humid and moist conditions favor pest proliferation (Wright 1992; Brenes-Arguedas et al. 2009). Our findings did not support this hypothesis, suggesting that infestation rates are also independent of precipitation regimes in savannas. This may be attributed to the species-level adaption to dry conditions which trigger a trade-off between resource investment in seeds versus chemical defenses against bruchid beetles' infestation. Infested seeds in water-stressed *Acacia* species have been found to possess high levels of non-protein amino acids such as pipecolic acid and djenkolic acid – potential compounds for defense against herbivory and infestation (Or and Ward 2004). Per Or and Ward (2004), these phenolic compounds are produced by seeds for defense. However, bruchid beetles may adapt a mechanism to profit from the compounds rendering the seeds vulnerable to more infestation. Additionally, another study by Kestring et al. (2009) which assessed the amount of phenolic compounds in infested and non-infested seeds found significantly higher levels in infested seeds than in non-infested. This suggests that these compounds are a result of induced rather than constitutive defense. For our case, rainfall seems not to be an important predictor of infestation and the mechanisms for seed defense against pests may be attributed by other factors such as masting which involve irregular mass production of seeds to overwhelm seed predators (Ashton et al. 1988; Mduma et al. 2007) and increase survival of remnant

seeds. Additionally, water-stress in our study species could not be measured and connected to infestation levels or chemical defense mechanisms.

Seed viability under laboratory conditions was consistently higher in *A. tortilis* than in *A. robusta* in both years (Fig. 4) and was strongly reduced by insect infestation. However, infestation did not completely inhibit germination in either species. While our findings contradict a study in *A. tortilis*, which reported no germination of infested seeds (Ahmed 2008), they agree with other studies demonstrating that beetle infestation reduced overall germination but promoted early germination in laboratory experiments (Mucunguzi 1995; Takakura 2002). Our hypothesis for these contradicting results is that seed mass and intensity of seed predation may play a role, where in one situation large seeds tend to have more food stored in cotyledons compared to small seeds (Leishman 2001; Shaw et al. 2002) and in another situation, seeds may have different intensities of infestation which involve the presence of one or several entry/exit holes made by beetles (Or and Ward 2004; Ahmed 2008). While the former means more food reserve than the beetles can exhaust and hence increasing the chances of germination, the latter may lead to multi-holed seeds' failure to germinate due to exhaustion of the food reserve (Ahmed 2008). In our case, seeds with more than one exit/entry hole were not very common (<1%); and we did not differentiate one hole from multiple holes. The negative relationship between infestation and seed mass was evident from the analysis. For *A. robusta,* seeds were consistently heavier than *A. tortilis* (Appendix 3*),* independent of infestation status. We also observed that *A. tortilis* seed mass declined with *MAP*, however this does not appear to affect seed viability and is not the case in *A. robusta* (Fig 5). As *A. tortilis* species dominate the dry sites of the ecosystem (Rugemalila et al. 2016)

and on average being lighter than *A. robusta* (Appendix 3), we theorize that low food reserves in their cotyledons may increase their vulnerability to infestation. Nevertheless, *A. tortilis* seeds found in the driest areas are heavier than those in mesic sites (Fig. 5a) suggesting a likely trade-off between investing in seed mass and maximizing germination potential. Tradeoffs between seed mass and seed survival strategy are common in many woody species, where larger seeds tend to increase germination and survival rates (Lahoreau et al. 2006). However, to offset species differences in seed viability, seeds of the same species need to be categorized by size and compared within species variation as a function of size. In our case the assessment was between species in which *A. tortilis* seeds seem to have overall higher viability potential and lower seed mass compared to *A. robusta*.

Generally, our study has produced key estimates for seed stage demographic rates which can be used for modelling tree dynamics in this system, and savannas in general. However, for that to be achieved, an integrated model of the entire tree life cycle is needed to rule out if the seed stage is limiting recruitment in trees. The current challenge involves accounting for high variation between years and species. As demographic rates seem to be independent of rainfall, suggesting trade-offs and physiological adaption, our results may be helpful in restoration ecology of *Acacia* species as they show how different potential seed stage bottlenecks in savanna influence seed demography, which may ultimately affect tree recruitment.

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Table 1. Summary table showing the total number of seeds used for viability test per infestation status per species in each year

	Acacia robusta		*Acacia tortilis*	
Year	# Infested	# Non-infested	# Infested	# Non-infested
2013	743	800	615	900
2014	700	700	500	1000

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Table 2. Model fits (AIC, the Akaike Information criterion) for the effect of *HEIGHT, SPECIES, BASAL* diameter and their interaction on infestation proportion using generalized linear mixed-effects models.

Fixed Effects Model†	ΔAIC∞	df
Intercept	12.1	3
SPECIES	10.1	4
SPECIES x HEIGHT	**0.0**	**6**
SPECIES + HEIGHT	**0.5**	**5**
SPECIES + BASAL	10.7	5

† See text for variable descriptions; in all cases *SITE* was treated as a random effect.

∞Models with the strongest support have lower values and are shown in bold

413 **Table 3.** Model fits for the effect of *MAP*, *MCP*, *SPECIES*, *YEAR* and their interaction on infestation proportion using generalized linear mixed-effects models.

Analysis	Fixed effects†	ΔAIC‡	df
Long term rainfall	Intercept only	95	3
	MAP	108	4
	SPECIES	98	4
	MAP + *SPECIES*	111	5
	MAP + *SPECIES* + *YEAR*	42	6
	MAP × *SPECIES*	119	6
	SPECIES* × *YEAR	**0**	**6**
	MAP + *SPECIES* + *YEAR* + *MAP* × *SPECIES* + *YEAR* × *SPECIES*	23	8
2013 rainfall	Intercept only	12	3
	MCP	23	4
	SPECIES	**0**	**4**
	MCP + *SPECIES*	13	5
	MCP x *SPECIES*	4	6
	MCP + *SPECIES* + *MCP* x *SPECIES*	4	6
2014 rainfall	Intercept only	18	3
	MCP	29	4
	SPECIES	**0**	**4**
	MCP + *SPECIES*	12	5
	MCP x *SPECIES*	23	6
	MCP + *SPECIES* + *MCP* x *SPECIES*	23	6

† See text for variable descriptions; in all cases SITE was treated as a random effect.

‡Models with the strongest support have lower values and are shown in bold

Table 4. Model fits for the effect of *MAP*, *SPECIES*, *INFESTATION* and their interaction on germination rates in year 2013 and 2014 using generalized linear mixed-effects models.

	2013		2014	
Fixed effect model†	ΔAICc‡	df	ΔAICc‡	df
Intercept	16	2	3	2
MAP	19	3	7	3
SPECIES	14	3	4	3
SPECIES + INFESTATION	7	4	2	4
SPECIES + INFESTATION + MAP	7	5	10	5
SPECIES * INFESTATION	**0**	**5**	**0**	**5**
*MAP * SPECIES*	19	5	18	5

† See text for variable descriptions; in all cases SITE was treated as a random effect.

‡Difference in Akaike Information Criterion (corrected for small sample sizes), compared to the best-fitting model

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Figure Legends:

Fig. 1. Map of Serengeti National park, NCA and surrounding game reserves, showing mean annual precipitation. b) Serengeti National Park map showing location of study plots and c) location of study trees.

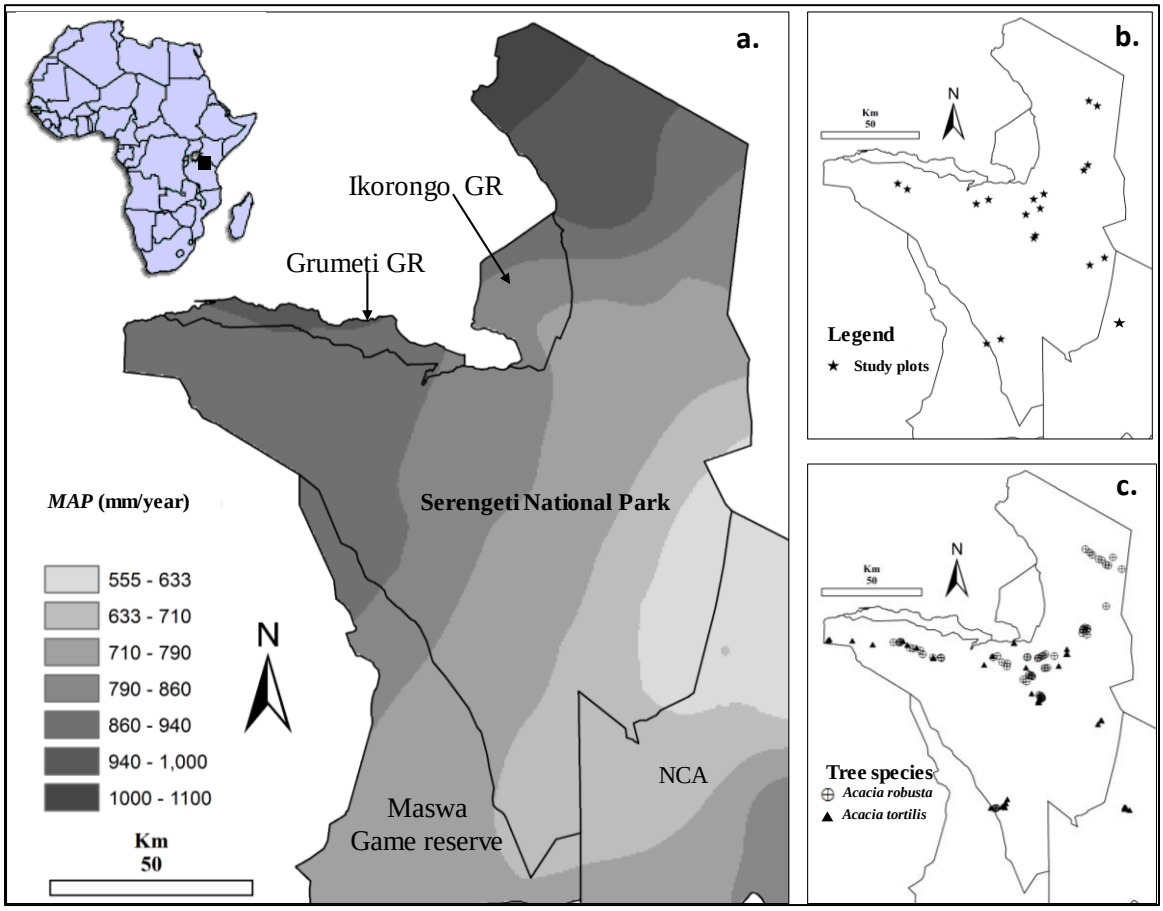
Fig. 2. Pod production as a function of *MAP* (mm. yr^{-1}) and *MCP* (mm. yr^{-1}) in *A. robusta* (acarob) (**a** and **c**) and *A. tortilis* (acator) (**b** and **d**). The grey circles represent the proportion of tree pod production per site

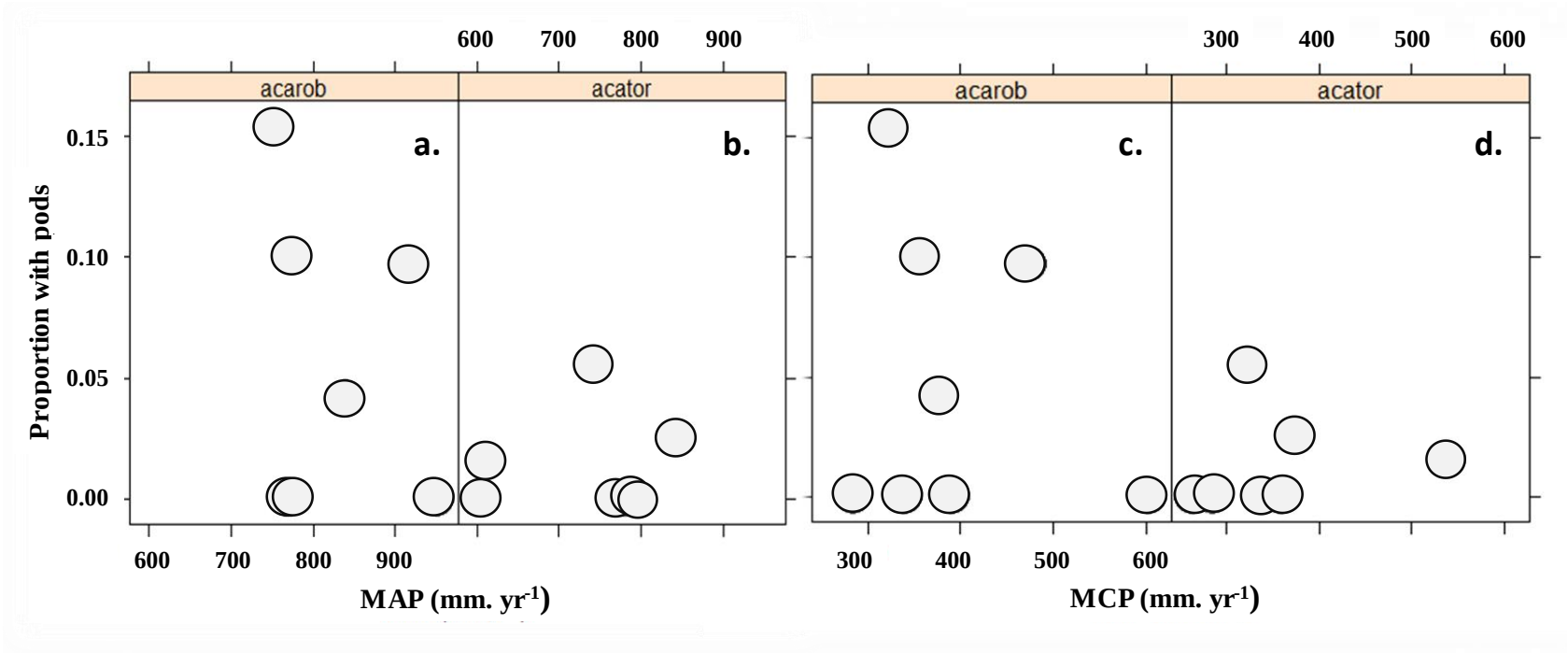
Fig. 3. Infestation proportions for *A. robusta* (acarob) and *A. tortilis* (acator) in 2013 and 2014 in Serengeti.

Fig. 4: Seed viability proportion in a) *A.robusta* (acarob) and *A. tortilis* (acator) for 2013 and 2014 non-infested seeds and b) for infested seeds.

Fig. 5. Seed mass proportion for non-infested seeds in a) *A. tortilis* ($R^2 = 0.25$) and b) *A. robusta* ($R^2 = 0.007$) as a function of *MAP* (mm. yr^{-1}).

Figures:


a.
Ikorongo GR
Grumeti GR
Serengeti National Park
NCA
Maswa
Game reserve
MAP (mm/year)
555 - 633
633 - 710
710 - 790
790 - 860
860 - 940
940 - 1,000
1000 - 1100
N
Km
50
b.
Legend
Study plots
c.
Tree species
Acacia robusta
Acacia tortilis


acarob
acator
a.
b.
c.
d.
Proportion with pods
0.15
0.10
0.05
0.00
600
700
800
900
300
400
500
600
MAP (mm. yr-1)
MCP (mm. yr-1)

438

439

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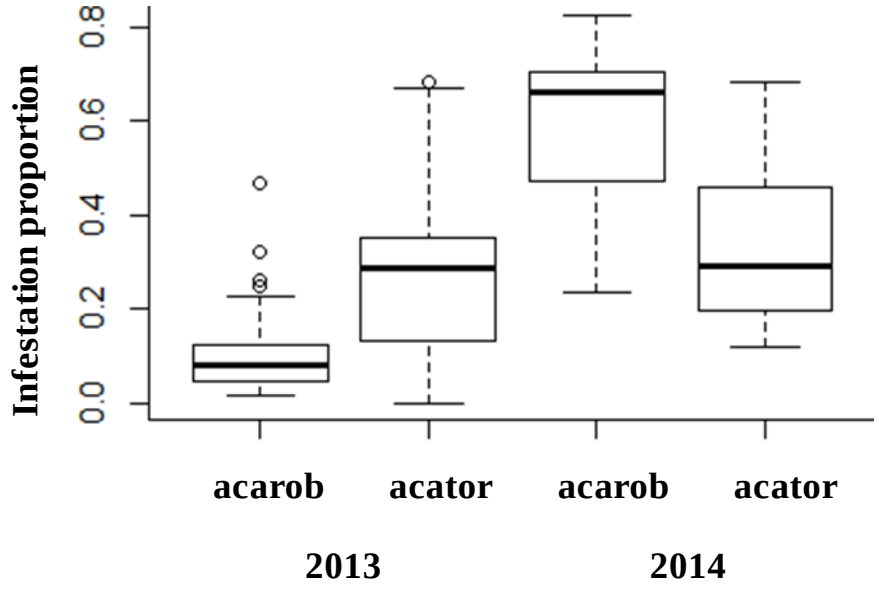
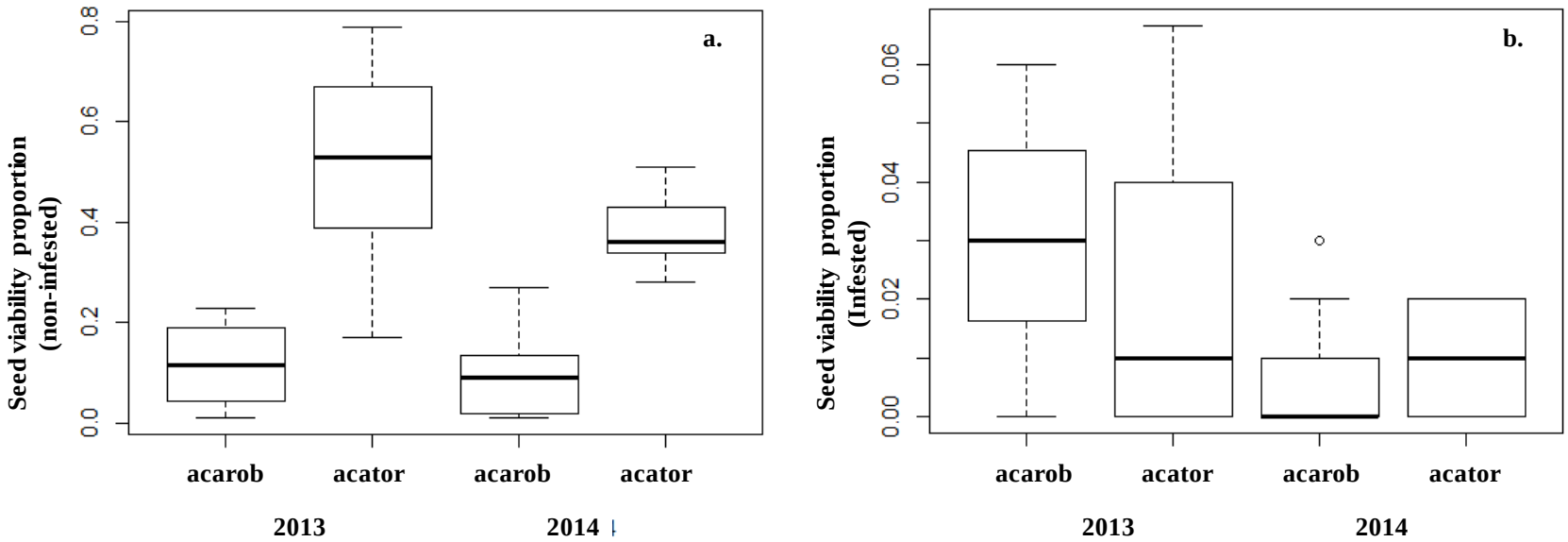

Infestation proportion
0.0
0.2
0.4
0.6
0.8
acarob
acator
acarob
acator
2013
2014

441

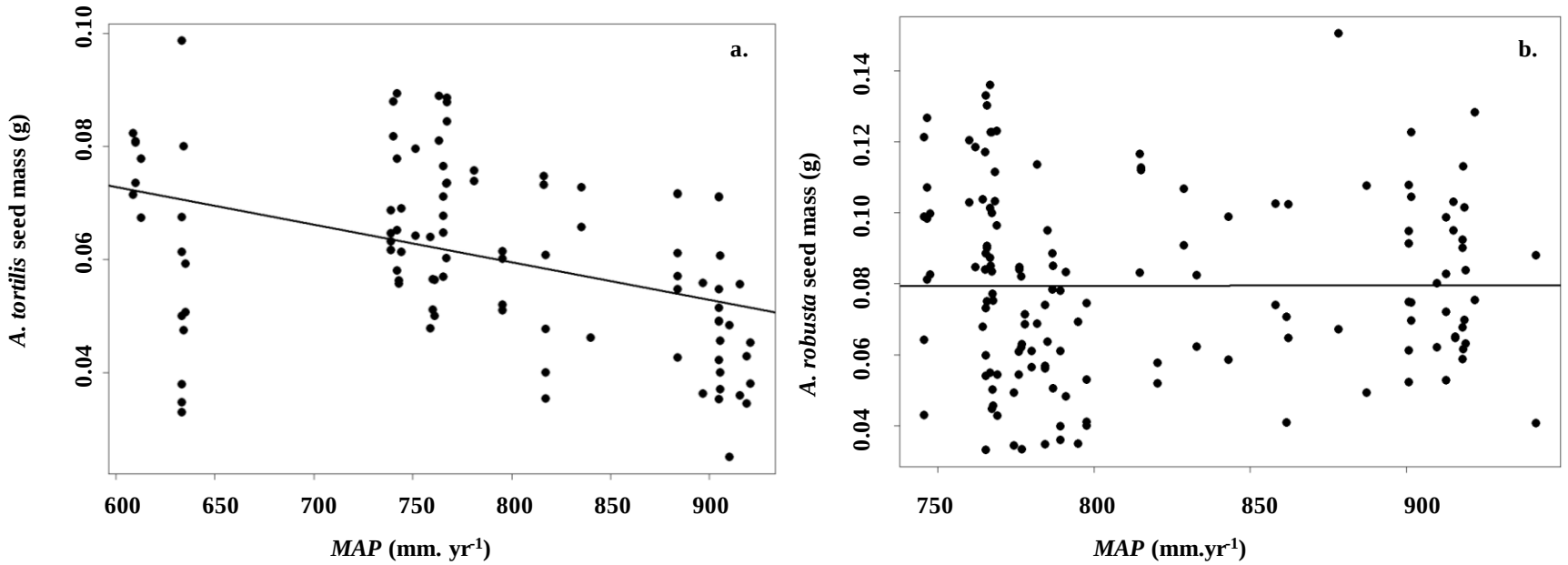
442

443


a.
Seed viability proportion (non-infested)
0.0
0.2
0.4
0.6
0.8
acarob
acator
acarob
acator
2013
2014
b.
Seed viability proportion (Infested)
0.00
0.02
0.04
0.06
acarob
acator
acarob
acator
2013
2014

444

445



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Appendix 1. Summary table showing the rainfall data used (*MAP* and *MCP*), number of trees that were included in pod production analysis.

SITE NAME	MAP (mm. yr^{-1})	MCP (mm. yr^{-1}) 2013	MCP (mm. yr^{-1}) 2014	# of trees (*Acacia robusta*)	# of trees (*Acacia tortilis*)
SOIT	601	222	304	0	22
NCA	614	879	200	0	39
SIMIYU	741	330	317	8	15
TAWIRI	768	190	379	28	10
TOGORO	768	435	348	39	1
BILILA	778	334	346	2	5
BANAGI	779	416	300	4	13
MUSABI	846	195	559	25	13
KIRAWIRA	917	615	334	27	0
KITALO	951	836	370	7	0

Appendix 2: Model fits (AIC, the Akaike Information criterion) for the effect of *MAP*, *SPECIES, INFESTATION, YEAR* and their interaction on seed mass of infested and non-infested seeds using generalized linear mixed-effects models

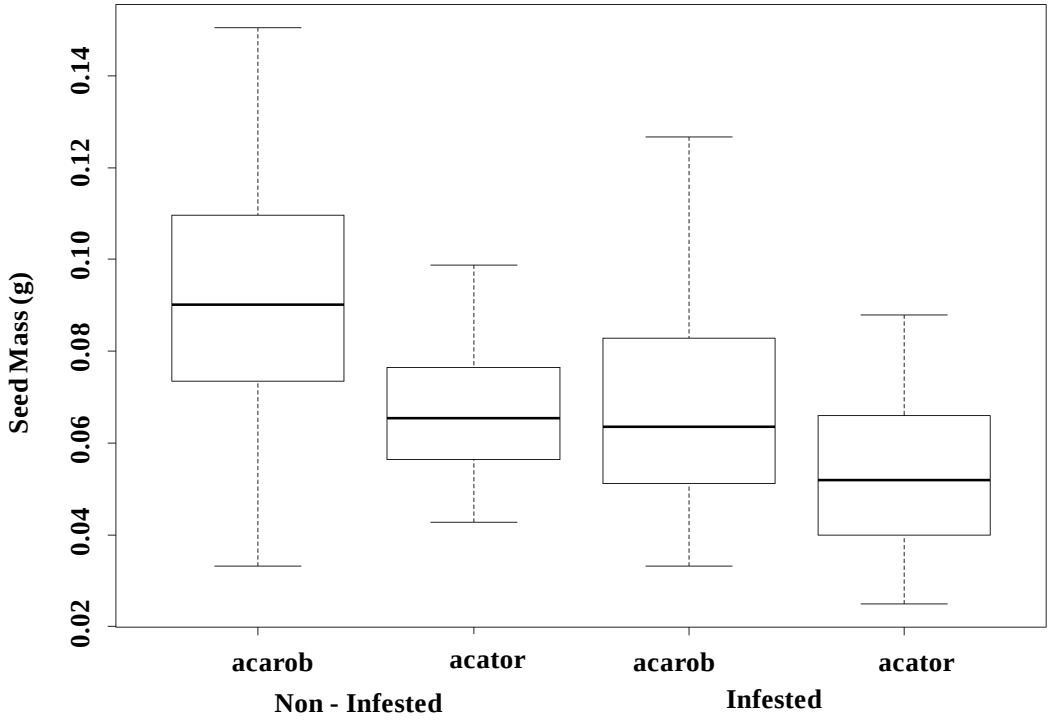
Analysis	Fixed effect model[†]	ΔAIC[∞]	df
Seed mass (all) ~ *MAP*	Intercept	74.4	3
	MAP	95.1	4
	SPECIES	45.6	4
	SPECIES + INFESTATION + YEAR	**0**	**6**
	SPECIES + MAP + INFESTATION + YEAR	20.4	7
	SPECIES x MAP + INFESTATION + YEAR	35.9	8
	SPECIES x INFESTATION +MAP + YEAR	24	7
	SPECIES x INFESTATION x MAP + YEAR	78.3	11
Seed mass (all) ~ 2013 *MCP*	intercept	49.1	5
	MCP	70	4
	SPECIES	10.5	4
	SPECIES + INFESTATION	**0**	**5**
	SPECIES + MCP + INFESTATION	18.6	6
	*SPECIES * MCP + INFESTATION*	39.2	7
	*SPECIES * INFESTATION + MCP*	25.8	7
	*SPECIES * INFESTATION * MCP*	88.8	10
Seed mass (non-infested) ~ 2013 *MCP*	Intercept	28	3
	MCP	49.3	4
	SPECIES	**0**	**4**
	SPECIES + MCP	20.1	5
	SPECIES x MCP	41.4	6

[†] See text for variable descriptions; in all cases SITE was treated as a random effect.

[∞]Models with the strongest support have lower values and are shown in bold

Appendix 3

Seed mass variation in *Acacia robusta* (acarob) and *Acacia tortilis* (acator) as a function of seed infestation status.



REFERENCES

Ahmed MAJ (2008) Effect of Bruchid Beetles (Burchidius Arabicus Decelle) Infestation on the Germination of Acacia tortilis (Forssk.) Hayne) Seeds American Journal of Environmental Sciences 4:285-288

Andersen GL, Krzywinski K, Gjessing HK, Pierce RH (2016) Seed viability and germination success of Acacia tortilis along land-use and aridity gradients in the Eastern Sahara Ecology and evolution 6:256-266

Anderson TM, Morrison T, Rugemalila D, Holdo R (2015) Compositional decoupling of savanna canopy and understory tree communities in Serengeti Journal of Vegetation Science 26:385-394 doi:10.1111/jvs.12241

Ashman TL et al. (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences Ecology 85:2408-2421

Ashton PS, Givnish T, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics The American Naturalist 132:44-66

Barnes ME (2001) Seed predation, germination and seedling establishment of Acacia erioloba in northern Botswana Journal of Arid Environments 49:541-554 doi:10.1006/jare.2001.0805

Baum CF (2008) Stata tip 63: Modeling proportions Stata Journal 8:299

Bond WJ (2008) What Limits Trees in C4Grasslands and Savannas? Annual Review of Ecology, Evolution, and Systematics 39:641-659 doi:10.1146/annurev.ecolsys.39.110707.173411

Brenes-Arguedas T, Coley PD, Kursar TA (2009) Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient Ecology 90:1751-1761

Bucini G, Hanan NP (2007) A continental-scale analysis of tree cover in African savannas Global Ecology and Biogeography 16:593-605

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media,

Clark CJ, Poulsen JR, Levey DJ (2013) Roles of seed and establishment limitation in determining patterns of Afrotropical tree recruitment PloS one 8:e63330

Danthu P, Ndongo M, Diaou M, Thiam O, Sarr A, Dedhiou B, Ould Mohamed Vall A (2003) Impact of bush fire on germination of some West African acacias Forest Ecology and Management 173:1-10 doi:http://dx.doi.org/10.1016/S0378-1127(01)00822-2

Danthu P, Roussel J, Dia M, Sarr A (1992) Effect of different pretreatments on the germination of Acacia senegal seeds Seed science and technology:111-117

De Bie S, Ketner P, Paasse M, Geerling C (1998) Woody plant phenology in the West Africa savanna Journal of Biogeography 25:883-900

De Menezes LC, Klein J, Kestring D, Rossi MN (2010) Bottom-up and top-down effects in a pre-dispersal seed predation system: are non-predated seeds damaged? Basic and Applied Ecology 11:126-134

Dempewolf J, Trigg S, DeFries R, Eby S (2007) Burned-area mapping of the Serengeti–Mara region using MODIS reflectance data Geoscience and Remote Sensing Letters, IEEE 4:312-316

ESRI (2013) ArcGIS 10.2.1 for Desktop, 10.2.1.3497 edn. ESRI Inc., Redlands, CA

February EC, Higgins SI, Bond WJ, Swemmer L (2013) Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses Ecology 94:1155-1164
Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net Effects of Large Mammals on Acacia Seedling Survival in an African Savanna Ecology 85:1555-1561 doi:10.1890/03-3060
Gordon-Gray KD (1965) Acacia robusta Burch. and Acacia clavigera E. Mey. in Natal, South Africa Brittonia 17:202-212
Greene D, Johnson E (1994) Estimating the mean annual seed production of trees Ecology:642-647
Harcombe PA (1987) Tree Life Tables University of California Press 37:557-568
Holdo RM, Anderson TM, Morrison T (2014) Precipitation, fire and demographic bottleneck dynamics in Serengeti tree populations Landscape Ecology 29:1613-1623
Holdo RM, Holt RD, Fryxell JM (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti Am Nat 173:431-445 doi:10.1086/597229
Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution Perspectives in Plant Ecology, Evolution and Systematics 1:32-46
Johnson KA, Goody RS (2011) The original Michaelis constant: translation of the 1913 Michaelis-Menten paper Biochemistry 50:8264
Kebbas S, Lutts S, Aid F (2015) Effect of drought stress on the photosynthesis of Acacia tortilis subsp. raddiana at the young seedling stage Photosynthetica 53:288-298
Kestring D, Menezes LC, Tomaz CA, Lima GP, Rossi MN (2009) Relationship among phenolic contents, seed predation, and physical seed traits in Mimosa bimucronata plants Journal of Plant Biology 52:569-576
Knight TM et al. (2005) Pollen limitation of plant reproduction: pattern and process Annual Review of Ecology, Evolution, and Systematics:467-497
Kyalangalilwa B, Boatwright JS, Daru BH, Maurin O, Bank M (2013) Phylogenetic position and revised classification of Acacia sl (Fabaceae: Mimosoideae) in Africa, including new combinations in Vachellia and Senegalia Botanical Journal of the Linnean Society 172:500-523
Lahoreau G, Barot S, Gignoux J, Hoffmann WA, Setterfield SA, Williams PR (2006) Positive effect of seed size on seedling survival in fire-prone savannas of Australia, Brazil and West Africa Journal of Tropical Ecology 22:719-722
Lamprey H, Halevy G, Makacha S (1974) Interactions between Acacia, bruchid seed beetles and large herbivores* African Journal of Ecology 12:81-85
Leishman MR (2001) Does the seed size/number trade-off model determine plant community structure? an assessment of the model mechanisms and their generality Oikos 93:294-302
LePage PT, Canham CD, Coates KD, Bartemucci P (2000) Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia Canadian Journal of Forest Research 30:415-427
Linzey AV, Washok KA (2000) Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe African Zoology 35:295-299

555 Loth PE, de Boer WF, Heitkönig IMA, Prins HHT (2005) Germination strategy of the
556 East African savanna tree Acacia tortilis Journal of Tropical Ecology 21:509-517
557 doi:10.1017/s026646740500252x
558 Luo Y, He F, Yu S (2013) Recruitment limitation of dominant tree species with varying
559 seed masses in a subtropical evergreen broad-leaved forest Community Ecology
560 14:189-195
561 Mduma SAR, Sinclair ARE, Turkington ROY (2007) The role of rainfall and predators in
562 determining synchrony in reproduction of savanna trees in Serengeti National
563 Park, Tanzania Journal of Ecology 95:184-196 doi:10.1111/j.1365-
564 2745.2006.01188.x
565 Michaelis L, Menten ML (1913) Die kinetik der invertinwirkung Biochem z 49:352
566 Midgley J, Bond W (2001) A synthesis of the demography of African acacias Journal of
567 Tropical Ecology 17:871-886
568 Miller JT, Seigler D, Mishler BD (2014) A phylogenetic solution to the Acacia problem
569 Taxon 63:653-658
570 Miller MF (1996) Acacia Seed Predation by Bruchids in an African Savanna Ecosystem
571 Journal of Applied Ecology 33:1137-1144
572 Miller MF, Coe M (1993) Is it advantageous for Acacia seeds to be eaten by ungulates?
573 Oikos 66:364-368
574 Moore G et al. (2011) The Acacia controversy resulting from minority rule at the Vienna
575 Nomenclature Section: Much more than arcane arguments and complex
576 technicalities Taxon 60:852-857
577 Mucunguzi P (1995) Effects of bruchid beetles on germination and establishment of
578 Acacia species African Journal of Ecology 33:64-70
579 Mucunguzi P, Oryem-Origa H (1996) Effects of heat and fire on the germination of
580 Acacia sieberiana D.C. and Acacia gerrardii Benth. in Uganda Journal of Tropical
581 Ecology 12:1-10 doi:10.1017/s0266467400009275
582 Münzbergová Z, Herben T (2005) Seed, dispersal, microsite, habitat and recruitment
583 limitation: identification of terms and concepts in studies of limitations Oecologia
584 145:1-8
585 Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their
586 determinants and consequences for recruitment Trends in Ecology & Evolution
587 15:278-285
588 Or K, Ward D (2003) Three-way interactions between Acacia, large mammalian
589 herbivores and bruchid beetles - a review African Journal of Ecology 41:257-265
590 doi:10.1046/j.1365-2028.2003.00451.x
591 Or K, Ward D (2004) The Effects of Seed Quality and Pipecolic and Djenkolic Acids on
592 Bruchid Beetle Infestation in Water Deficit-Stressed Acacia Trees Journal of
593 Chemical Ecology 30:2297-2307 doi:10.1023/b:joec.0000048790.85830.79
594 Pinheiro J, Bates D, DebRoy S, Sarkar D (2011) R Development Core Team. 2010. nlme:
595 linear and nonlinear mixed effects models. R package version 3.1-97 R
596 Foundation for Statistical Computing, Vienna
597 R Development Core Team (2011) R: A language and environment for statistical
598 computing. R Foundation for Statistical Computing, Vienna, Austria
599 Rodríguez-Pérez J, Wiegand K, Ward D (2011) Interaction between ungulates and
600 bruchid beetles and its effect on Acacia trees: modeling the costs and benefits of

601 seed dispersal to plant demography Oecologia 167:97-105 doi:10.1007/s00442-
602 011-1964-6
603 Rohner C, Ward D (1999) Large Mammalian Herbivores and the Conservation of Arid
604 Acacia Stands in the Middle East Conservation Biology 13:1162-1171
605 doi:10.1046/j.1523-1739.1999.97300.x
606 Rugemalila DM, Anderson TM, Holdo RM (2016) Precipitation and Elephants, Not Fire,
607 Shape Tree Community Composition in Serengeti National Park, Tanzania
608 Biotropica doi:10.1111/btp.12311
609 Salazar A, Goldstein G, Franco AC, Miralles-Wilhelm F (2011) Seed limitation of woody
610 plants in Neotropical savannas Plant Ecology 213:273-287 doi:10.1007/s11258-
611 011-9973-4
612 Sankaran M et al. (2005) Determinants of woody cover in African savannas Nature
613 438:846-849 doi:10.1038/nature04070
614 Sankaran M, Ratnam J, Hanan NP (2004) Tree-grass coexistence in savannas revisited -
615 insights from an examination of assumptions and mechanisms invoked in existing
616 models Ecology Letters 7:480-490 doi:10.1111/j.1461-0248.2004.00596.x
617 Seghieri J, Floret C, Pontanier R (1995) Plant phenology in relation to water availability:
618 herbaceous and woody species in the savannas of northern Cameroon Journal of
619 Tropical Ecology 11:237-254
620 Shaw MT, Keesing F, Ostfeld RS (2002) Herbivory on Acacia Seedlings in an East
621 African Savanna Oikos 98:385-392 doi:10.1034/j.1600-0706.2002.980303.x
622 Sinclair A, Mduma SA, Arcese P (2000) What determines phenology and synchrony of
623 ungulate breeding in Serengeti? Ecology 81:2100-2111
624 Svenning JC, Wright SJ (2005) Seed limitation in a Panamanian forest Journal of
625 Ecology 93:853-862
626 Takakura K (2002) The specialist seed predator Bruchidius dorsalis (Coleoptera:
627 Bruchidae) plays a crucial role in the seed germination of its host plant, Gleditsia
628 japonica (Leguminosae) Functional Ecology 16:252-257
629 Thiele KR et al. (2011) The controversy over the retypification of Acacia Mill. with an
630 Australian type: a pragmatic view Taxon 60:194-198
631 Thomson FJ, Moles AT, Auld TD, Kingsford RT (2011) Seed dispersal distance is more
632 strongly correlated with plant height than with seed mass Journal of Ecology
633 99:1299-1307
634 Thomson FJ, Moles AT, Auld TD, Ramp D, Ren S, Kingsford RT (2010) Chasing the
635 unknown: predicting seed dispersal mechanisms from plant traits Journal of
636 Ecology 98:1310-1318
637 Walters M, Milton SJ (2003) The production, storage and viability of seeds of Acacia
638 karroo and A. nilotica in a grassy savanna in KwaZulu-Natal, South Africa
639 African Journal of Ecology 41:211-217
640 Warton DI, Hui FK (2011) The arcsine is asinine: the analysis of proportions in ecology
641 Ecology 92:3-10
642 Williams RJ, Myers BA, Eamus D, Duff GA (1999) Reproductive Phenology of Woody
643 Species in a North Australian Tropical Savanna1 Biotropica 31:626-636
644 Witkowski E, Garner R (2000) Spatial distribution of soil seed banks of three African
645 savanna woody species at two contrasting sites Plant Ecology 149:91-106

Wright SJ (1992) Seasonal drought, soil fertility and the species density of tropical forest plant communities Trends in ecology & evolution 7:260-263
Wyatt JL, Silman MR (2004) Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities Oecologia 140:26-35